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A NEW ARTIODACTYL (MAMMALIA) FROM THE EOCENE PONDAUNG SANDSTONES, BURMA

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ABSTRACT

Reanalysis of artiodactyl material from the late middle Eocene Pondaung sandstones of Burma indicates the presence of a new genus assignable to the Helohyidae. A single specimen, previously described as an anthracotheriid and placed in the genus *Anthracokeryx,* is described below as *Pakkokuhyus,* n. gen. *Pakkokuhyus,* n. gen., represents the most southerly occurrence of the family Helohyidae. The new Burmese genus also has resemblances to the putative raoellid *Haqueina* from the early or middle Eocene of Pakistan.

INTRODUCTION

The Pondaung Beds of the Chindwin-Irrawaddy Basin of Burma (also called Myanmar) have long been known for the diverse anthracotheriid artiodactyl fauna found there (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). The only other artiodactyl family previously reported from this fauna is the Gelocidae (*Indomeryx cotteri,* Pilgrim, 1928; Colbert, 1938; Russell and Zhai, 1987). Reexamination of Pondaung anthracotheriid fossils in the collections of the Geological Survey of India (GSI) has revealed the presence of an additional artiodactyl in the Pondaung fauna. Collected in 1920 or 1921 by H. M. Lahirii and B. B. Gupta and previously described as *Anthracokeryx* ? *lahirii* (Pilgrim, 1928), this species is now recognized as a new genus of the family Helohyidae. This new genus represents the most southerly occurrence of helohyids and also bears resemblances to the putative raoellid *Haqueina.*

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla
Family Helohyidae Marsh 1877
Pakkokuhyus, new genus

Anthracokeryx? Pilgrim, 1928; Colbert, 1938.

Type and Only Species.—*Pakkokuhyus lahirii* (Pilgrim, 1928).

Etymology.—Named for the Pakkoku District, where the type specimen was found, and *hyus,* from the Greek *hys,* pig.

Distribution.—Pondaung Formation, late middle Eocene.

Diagnosis.—Differs from the helohyid genera *Gobiohyus* from the Mongolian middle Eocene and *Helohyus* from the early middle Eocene (Bridgerian) of North

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America in having: molar paraconids apparently lacking; a continuous labial cingulid on M_3; a basally inflated crown; more bunodont and less conical cusps; stronger labial cingulids on M_1–M_2; less pronounced ectoflexid; absolutely and relatively greater mandibular depth; shorter and less distinct hypoconulid loop on M_3. Further differs from *Gobiohyus* in having relatively higher crowns and from *Helohyus* in having a stronger hypoconulid on the distal cingulid and in lacking accessory cuspulids on the hypoconulid loop. Differs from the possible raoellid *Haqueina* in having: a stronger hypoconulid on the distal cingulid; a weaker and less constricted hypoconulid "loop"; a single M_3 hypoconulid; postcristid lacking; and weaker hypolophid and cristid obliqua. Differs from anthracotheriids in its smaller size and in having a straight hypolophid; a short M_3 hypoconulid loop; and in lacking a premetacristid. Differs from all of the above in having entoconid slightly posterior to hypoconid.

Pakkokuhyus lahirii (Pilgrim, 1928)
Fig. 1A–B

Anthracokeryx? lahirii Pilgrim 1928, plate 4, figure 4, 4a; Colbert 1938.

Type and Only Specimen.—Geological Survey of India (GSI) B-766, right mandibular fragment with M_1–M_3.

Type Locality.—"K21-315, three furlongs [approximately 0.6 km] N.W. [northwest] of Thanudaw village, Myaing Township, Pakkoku District, Burma." "K21" is a section designation on Geological Survey of India maps of the region.

Diagnosis.—As for genus.

Description.—Measurements (in mm) for GSI B-766 are: M_1 length, 7.1; M_1 trigonid width, 4.9; M_1 talonid width, 5.1; M_2 length, 8.6; M_2 trigonid width, 6.6; M_2 talonid width, 7.2; M_3 length, 12.5; M_3 trigonid width, 7.5; M_3 talonid width, 7.2.

The molars are basically quadritubercular and increase in size from front to back. There is no apparent paraconid; however, the degree of wear on M_1 and M_2 makes it virtually impossible to determine whether a small paraconid may have been present on either of these teeth. A small hypoconulid is present on M_1 and M_2, and a single hypoconulid and "loop" are present on M_3. The cusps are bunodont, and the crowns are of medium height. The bases of the crowns are inflated, and the labial surfaces slope medially. The protoconid and metaconid are higher than the talonid cusps and are situated close together, with the metaconid being the larger of the two. The protoconid is slightly anterior to the metaconid, and the two cusps are joined by a looping paracristid that extends along the anterior face of the trigonid toward the mesial cingulid, but is separated from the cingulid by a 1.2 mm gap. A very short protocristid joins the two trigonid cusps. Both the anterior and posterior faces of the trigonid are almost vertical.

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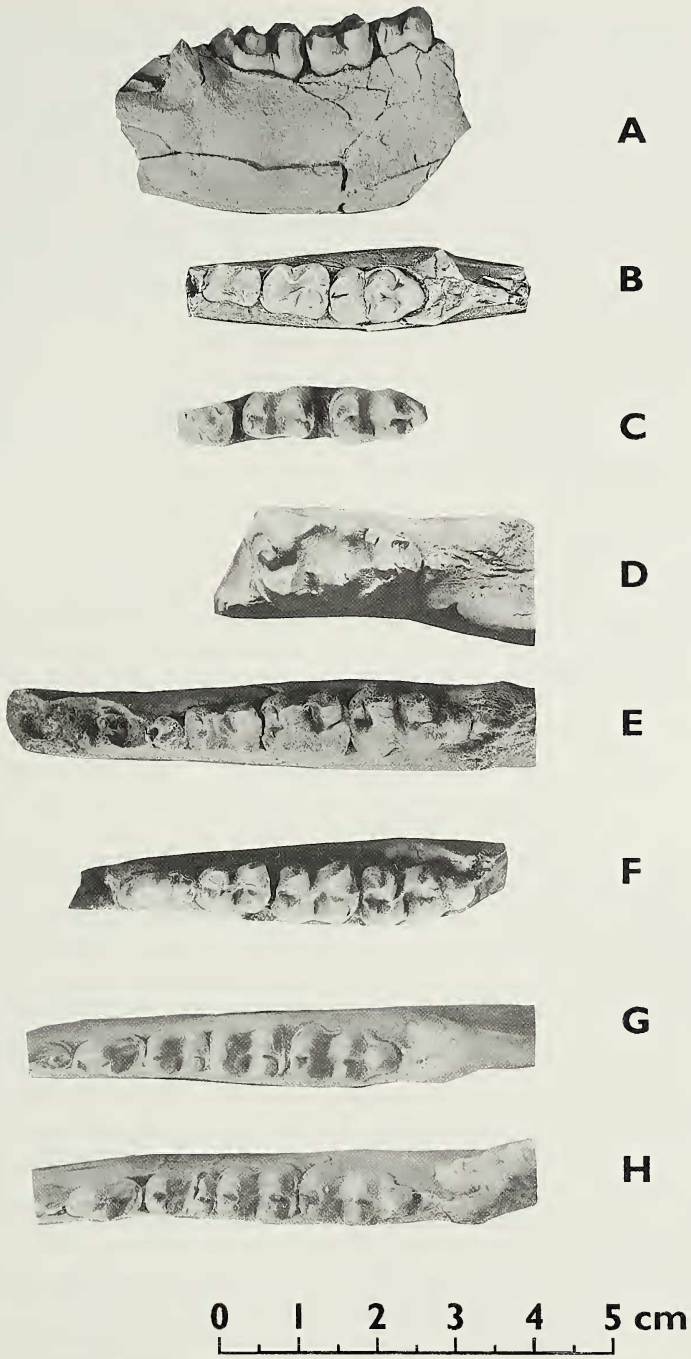
Fig. 1.—A. Lateral view of GSI B-766, holotype of *Pakkokuhyus lahirii.* Occlusal views of: B. *P. lahirii,* GSI B-766, right mandibular fragment with M_1–M_3; C. *Helohyus validus,* AMNH 10011, associated? isolated right M_2–M_3, left M_1 from near Henry's Fork, Sweetwater County, Wyoming; D. *Helohyus lentus,* AMNH 12150, left mandibular fragment with M_3 from the Bridger Formation (D3), Henry's Fork Hill, Sweetwater County, Wyoming; E. *Gobiohyus orientalis,* AMNH 20248, left mandibular fragment with M_1–M_3 from Irdin Manha Formation, Telegraph Line Camp, Chahar Province,



Inner Mongolia, China; F. *G. orientalis,* AMNH 20250, right mandibular fragment with P_4–M_3 from same locality as given for AMNH 20248; G. *G. orientalis,* AMNH 26282, right mandibular fragment with P_4–M_3 from same locality as given for AMNH 20248; H. *G. orientalis,* AMNH 26280, right mandibular fragment with C, P_2–M_3, only P_4–M_3 shown, from same locality as given for AMNH 20248.

The talonids of M_1–M_2 are somewhat wider than the trigonids and open lingually. The hypoconid is slightly anterior to the entoconid and is connected to it by a low, straight hypolophid. The cristid obliqua is lingually oriented and meets the posterior trigonid wall at the midline of the tooth. The hypoconulid on M_2 is connected to the hypoconid by a short, well-developed postcristid. Mesial and distal cingulids are weakly developed, and there is a short labial cingulid between the hypoconid and protoconid on M_1 and M_2.

The first molar is worn, showing heaviest wear on the anterior wall of the trigonid, along the cristid obliqua, and on the lingual side of the entoconid such that the upper half of the crown is missing, with the exception of a small pool of enamel at the bottom of the talonid basin. However, in its preserved features it appears to be a smaller version of the second molar.

The third molar has a large hypoconulid. A low but prominent postcristid joins this cusp to the hypoconid, cutting off a small, lingually open hypoconulid basin within the hypoconulid "loop." A strong labial cingulid is present from the hypoconulid to the base of the protoconid.

The mandible is robust, measuring 19.2 mm at its greatest depth, beneath M_2. The inferior border of the ramus angles gently upward from this point, and there is no indication of an expanded mandibular angle similar to that seen in *Gobiohyus* or anthracotheriids. The base of the ascending ramus is preserved, and the anterior portion of the masseteric fossa is present. This fossa forms a deep depression in the ramus, and its lowest level of insertion is marked by a distinct crest approximately 13 mm from the lower border of the mandible. At its most anterior extent, the fossa forms a sharp crest at the base of the ascending ramus.

Discussion

Age of Pakkokuhyus lahirii

The Pondaung mammalian fauna occurs within a thick succession of marine and continental rocks that were deposited throughout the Eocene and are now exposed in the Chindwin-Irrawaddy Basin. The middle Eocene to upper Eocene portions of this sequence have been termed, from oldest to youngest, the Tabyin clay, the Pondaung sandstones, and the Yaw shale. The term "formation" has been applied to these strata by some workers (e.g., Bender, 1983). However, this term has not been used in its modern sense, that is, a defined lithostratigraphic unit. There are few clear boundaries between the Eocene "formations" of the Chindwin-Irrawaddy Basin, except at the lower boundary of the Yaw shale, where there is a distinct lithological break with the underlying Pondaung sandstones (Stamp, 1922; Cotter and Clegg, 1938; Bender, 1983). For this reason, the informal names given above are employed here.

Pakkokuhyus lahirii occurs within the upper part of the Pondaung sandstones, in a sequence of paleosols that represents virtually the only continental deposits in the Eocene succession. These continental deposits have traditionally been considered late Eocene in age, largely on the basis of the "degree of evolution" of their artiodactyl and perissodactyl taxa when compared with related forms in Africa, North America, China, and Mongolia (Pilgrim, 1928; Colbert, 1938; Bender, 1983). The only constraints on the age of the Pondaung sandstones are the relationships of these rocks to the underlying marine Tabyin clay and overlying marine Yaw shale, which can be broadly correlated to European Standard Stages based on their invertebrate faunas.

The Tabyin clay has been assigned to the Lutetian Stage (early middle Eocene) by correlation with the Khirthar Stage in India (see Eames, 1951, and Gingerich and Russell, 1990, for comments on the correlation of the Indo-Pakistan sequences with European Standard Stages). The Yaw shales have been considered Ludian/Priabonian (upper Eocene) in age (Stamp, 1922; Cotter and Clegg, 1938; Bender, 1983), although an older age may be possible. The Yaw shales have been correlated to the Nanggulan Formation of Java (e.g., Holland, 1926) based on the common occurrence of *Discocylina*. Studies of mollusks (Zachello, 1984), calcareous nannoplankton (Okada, 1981), and planktonic foraminifera (Purnamaningsih and Harsono, 1981) from the Nanggulan Formation indicate that the *Discocylina* beds span the latest Lutetian through Priabonian. Thus, the Yaw shales may be older than Priabonian. These age assessments for the marine strata of Burma suggest a Bartonian (late middle Eocene) age for the Pondaung sandstones and fauna based on their intermediate stratigraphic placement. The justification for a Bartonian-equivalent age for the Pondaung fauna and its correlation to other important mammalian faunas in Asia is discussed in more detail in Holroyd and Ciochon (1994).

Comparisons with Other Bunodont Artiodactyla

In Pilgrim's (1928) original description, he compared the type and only specimen of *Pakkokuhyus lahirii* favorably with the helohyid genera "*Lophiohyus*" (=*Helohyus*) from the North American Bridgerian Land Mammal Age (LMA) and *Gobiohyus* from the Asian Irdinmanhan LMA. He recognized that this species probably did not belong in the genus *Anthracokeryx*. However, he believed the molar pattern of GSI B-766 to be typical of anthracotherioids, and so did not ally it with the helohyids. Colbert (1938) reiterated Pilgrim's remarks and agreed that the specimen probably belonged to a different genus than *Anthracokeryx*.

Pakkokuhyus is clearly not an anthracotheriid. *Anthracokeryx, Anthracothema, Siamotherium,* and other bunodont Asian anthracotheriids are characterized by the presence of strong, mesiolabially-directed premetacristids, well-separated metaconids and protoconids that are subequal in size, cristids oblique that ascend the posterior trigonid wall, V-shaped hypolophids, well-developed and posteriorly-extended M_3 hypoconulid loops, common occurrence of a double hypoconulid on M_3, and larger body size (see descriptions in Pilgrim, 1928, and Suteethorn et al., 1988). *Pakkokuhyus* lacks all of these features.

Pakkokuhyus shows greater affinities with the Helohyidae (Fig. 1C–H), composed of *Helohyus* from the North American Bridgerian LMA and *Gobiohyus* from the Asian Irdinmanhan LMA. In its size, degree of bunodonty, and cingular development, *Pakkokuhyus* is most similar to *Helohyus* spp., and is matched by *H. lentus* (Fig. 1E) in the relative size of the hypoconulid. Similarities to *Gobiohyus* (Fig. 1F–H, *G. orientalis*) are not so marked, although the reduction of the paraconid in *Gobiohyus* could be considered a shared resemblance. However, given the limited number of specimens of most species of *Helohyus* (see Sinclair, 1914) and of *Pakkokuhyus lahirii,* it is not realistic to attempt to determine possible relationships among these species.

Although *Pakkokuhyus* clearly shows greatest similarities to helohyids, among Old World artiodactyls, *Pakkokuhyus* also bears similarity to the late early or early middle Eocene *Haqueina haquei* from Ganda Kas in Pakistan. *Pakkokuhyus* and *Haqueina* are similar in size and have comparably bunodont dentitions, lingually-oriented cristids oblique, small but distinct M_2 hypoconulids, metacon-

ids slightly smaller than protoconids, lingually open talonid basins, distinct and straight M_3 hypolophids, and entoconids subequal in size and height to the hypoconid. However, *Haqueina* is of problematic familial affinities. Originally described as a dichobunid by Dehm and Oettingen-Spielberg (1958), it has more recently been allied with the Raoellidae (Sahni et al., 1981; Thewissen et al., 1987). However, as noted by Thewissen et al. (1987), *Haqueina* differs from raoellids in several features. Features distinguishing *Haqueina* from raoellids are those, enumerated above, that are shared with *Pakkokuhyus.* Thus, it is possible that *Haqueina* may be better allied with helohyids, and that it, along with *Pakkokuhyus,* represents a southern and Tethyan element in a family better known from its northern representatives.

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Literature Cited

Bender, F. 1983. The Geology of Burma. Beiträge zur Regionalen Geologie der Erde, Band 16, 293 pp.

Colbert, E. 1938. Fossil mammals from Burma in the American Museum of Natural History. Bulletin, American Museum of Natural History, 74:255–436.

Cotter, G. de P., and E. L. G. Clegg. 1938. Geology of parts of Minbu, Myingyan, Pakkoku, and lower Chindwin Districts, Burma. Memoirs of the Geological Survey of India, 72:1–136.

Dehm, R., and T. Oettingen-Spielberg. 1958. Paläontologische und geologische Untersuchungen im Tertiar von Pakistan. 2. Die mitteleocänen Saugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. Bayerische Akademie der Wissenschaften (Mathematisch-Naturwissenschaftliche Klasse), Abhandlungen, Neue Folge, Heft 91:1–58.

Eames, F. E. 1951. A contribution to the study of the Eocene in western Pakistan and western India: D. Discussion of the faunas of certain standard sections, and their bearing on the classification and correlation of the Eocene in western Pakistan and western India. Quarterly Journal, Geological Society of London 107:173–200.

Gingerich, P. D., and D. E. Russell. 1990. Dentition of early Eocene *Pakicetus* (Mammalia, Cetacea). Contributions from the Museum of Paleontology, The University of Michigan, 28:1–20.

Holland, T. H. 1926. Classification and correlation of Burma Tertiaries with those of Java and western India. Memoirs of the Geological Survey of India, 51:27–54.

Holroyd, P. A., and R. L. Ciochon. 1994. Relative ages of Eocene primate-bearing deposits of Asia. Pp. 123–141, *in* Anthropoid Origins (J. G. Fleagle and R. F. Kay, eds.), Plenum Press, New York.

Marsh, O. C. 1877. Introduction and succession of vertebrate life in America. American Journal of Science, Series 3, 14:337–378.

Okada, H. 1981. Calcareous nannofossils of Cenozoic formations in central Java. Pp. 25–34, *in* Micropaleontology, Petrology and Lithostratigraphy of Cenozoic Rocks of the Yogyarkarta Region, Central Java (T. Saito, ed.), Yamagata.

Pilgrim, G. E. 1928. The Artiodactyla of the Eocene of Burma. Memoirs of the Geological Survey of India, New Series, 8:1–39.

Pilgrim, G. E., and G. de P. Cotter. 1916. Some newly discovered Eocene mammals from Burma. Records of the Geological Survey of India, 48:42–82.

Purnamaningsih, S., and P. Harsono. 1981. Stratigraphy and planktonic foraminifera of the Eocene–Oligocene Nanggulan Formation, central Java. Publications, Geological Research and Development Centre, Paleontological Series, 1:9–28.

Russell, D. E., and Zhai Ren-jie. 1987. The Paleogene of Asia: Mammals and stratigraphy. Mémoires de Muséum National d'Histoire Naturelle, Sciences de la Terre, 52:1–488.

Sahni, A., S. B. Bhatia, J.-L. Hartenberger, J.-J. Jaeger, K. Kumar, J. Sudre, and M. Vianey-Liaud. 1981. Vertebrates from the Subathu Formation and comments on the biogeography of

Indian subcontinent during the early Paleogene. Bulletin, Societé Géologique de France, 23:689–695.

SINCLAIR, W. J. 1914. A revision of the bunodont Artiodactyla of the middle and lower Eocene of North America. Bulletin, American Museum of Natural History, 33:267–295.

STAMP, L. D. 1922. An outline of the Tertiary geology of Burma. Geological Magazine 59:481–501.

SUTEETHORN, V., E. BUFFETAUT, R. HELMCKE-INGAVAT, J.-J. JAEGER, AND Y. JONGKANJANSOONTORN. 1988. Oldest known Tertiary mammals from Southeast Asia: Middle Eocene primate and anthracotheres from Thailand. Neues Jahrbuch für Geologie und Paläontologie, 9:563–570.

THEWISSEN, J. G. M., P. D. GINGERICH, AND D. E. RUSSELL. 1987. Artiodactyla and Perissodactyla (Mammalia) from the early–middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, The University of Michigan, 27:247–274.

ZACHELLO, M. 1984. The Eocene mollusc fauna from Nanggulan (Java) and its palaeogeographic bearing. Memoire di Scienze Geologiche, 34:377–390.